

## CARBON UPTAKE AND ALLOCATION IN SUBALPINE ECOSYSTEMS

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Subalpine forests of the western slopes of the Cascade Mountains and the British Columbia Coast Range occupy an environment substantially different from those of most other subalpine forests of North America. These forests tend to be dominated by Pacific silver fir (Abies amabilis) and generally lie between 600 m and 1600 m in elevation. Climate in this elevation range is cool and wet and the growing season is short because of deep persistent snow accumulations. However, the soils seldom freeze. This combination of low soil temperatures, heavy snow accumulation, and short growing season manifests itself in low aboveground productivity, in heavy forest floor accumulations even in young stands (Grier et al. 1981), and low nutrient mineralization rates (Meier 1982, Vitousek et al. 1982).

In 1976 an intensive research program focused on determining factors influencing productivity of Abies amabilis zone forests was started in the College of Forest Resources, University of Washington. Much of this research was conducted at the Findley Lake Research Area; a study site located about 60 km southeast of Seattle, Washington, in the Cascade Mountains. This research program was a departure from most previous productivity research in that dry matter production taking place belowground received as much emphasis as that occurring above the soil.

The major hypothesis underlying this research was that changes in soil nutrient availability can significantly alter the above- to belowground production balance of an ecosystem. The basic idea was that mineral nutrients originally obtained from the soil would be progressively immobilized in the heavy surface, organic accumulations characteristic of this cold, wet, environment. We postulated that trees would respond to a steadily declining nutrient availability by progressively increasing their reliance on fine root activity and mycorrhizae. In effect, the stand would respond to progressively declining nutrient availability by shifting from aboveground production of wood, bark, and foliage to belowground production of fine roots and mycorrhizae. Our objective was to test this hypothesis at least for forests of the Abies amabilis zone of Washington.

### Abies amabilis Zone

The Abies amabilis zone is a subalpine forest zone occupying middle to upper elevations along the western slopes of the Oregon and Washington Cascades, the Olympic Mountains, Vancouver Island, and the British Columbia Coast Range.

The lower elevation limit of this forest zone ranges from about 1000 m in Oregon to about 600 m in southern British Columbia. Although Abies amabilis as a species ranges to near sea level on the Olympic Peninsula and Vancouver Island, the Abies amabilis zone is considered to be an upper-slope or subalpine forest type (Franklin and Dyrness 1973).

Vegetation of the Abies amabilis zone has been described in detail for Oregon and Washington by Franklin and Dyrness (1973) and for British Columbia in Krajina (1970). Briefly, the dominant climax tree species is Abies amabilis; common associates are Pseudotsuga menziesii, Abies procera, Tsuga heterophylla, Tsuga mertensiana, Pinus monticola, and Chamaecyparis nootkatensis.

Understory vegetation commonly includes a variety of species of Vaccinium, Menziesia feruginea, Cornus canadensis, Clintonia uniflora, and Xerophyllum tenax.

Soils of the Abies amabilis zone are primarily spodosols ranging from haploorthods (Brown podzolic soils) in the southern (Oregon) part of the zone to cryorthods (Podzols) in the northern. Inceptisols are also common throughout the Abies amabilis zone.

The climate of this forest zone is cool and wet. Precipitation ranges from 2000 to 3000 mm per year with less than 10% falling between May and September. Over 80% of the annual precipitation is snow. Predawn leaf water potentials less than -6 bars are seldom seen in trees of this zone (Zobel et al. 1976, Teskey 1982).

Mean annual temperature averages about 5.6°C; July temperatures average about 14°C while January temperatures average about -3°C. Even in midwinter, soil temperatures are above freezing (0.5°C).

### Findley Lake Research Area

The Findley Lake Research Area is located in the Abies amabilis zone of the Washington Cascade Mountains about 65 km southeast of Seattle, on the City of Seattle, Cedar River Watershed. A detailed description of soils, topography, and vegetation is given by Grier et al. (1981). Soils here are representative of the Abies amabilis zone of the Northern Cascades; soils are primarily podzols with thick mor-type forest floors. Vegetation is perhaps more representative of the southern Abies amabilis zone. The Abies amabilis-Vaccinium membranaceum-Xerophyllum tenax association, so common in Oregon, is the most prevalent vegetation type around Findley Lake. However, the herb-rich Abies amabilis-Tiarella unifoliata association common to the North Cascades is also well represented.

The Findley Lake Research Area was originally established in 1971 by the Coniferous Forest Biome, US/IBP, as a site for study of land-water interactions. The present research program was started in 1977.

Findley Lake is located in a north-facing abandoned glacial cirque. Forest cover is primarily mature *Abies amabilis* averaging about 185 years old.

Young stands of *Abies amabilis*, ranging from 0 to about 30 years old established after logging, are also present. Plots for the study described here were established in stands that were 26 and 180 years old when research started.

#### Methods

The procedures used for determining biomass distribution and net primary production are described in detail by Grier et al. (1981) and Grier and Milne (1981). A brief outline is given here for the reader's convenience.

**Plots.** Eight 25 m x 25 m study plots were surveyed and marked in the mature stand; forty-eight 6 m x 6 m plots were established in the young stand. Stand characteristics are given in Table 1.

Table 1.--Topography, stand structure, and climate of study sites in the *Abies amabilis* zone. Findley Lake research area, Washington Cascade Mountains.

	Young stand	Mature stand
<b>Topography</b>		
Elevation (m)	1140	1140
Slope	5°-12°	0°-5°
Aspect	SW	SW
<b>Stand Characteristics</b>		
Mean age (yr)	23	180
Basal area (m <sup>2</sup> /ha)	45.7	74.3
Density (stems/ha)	110,500	510
Height of dominants (m)	2.5	39.0
Diameter range (cm)	0.5-7.0	5.0-103.9
<b>Climate</b>		
Mean annual temperature (°C)		5.4
Mean July temperature (°C)		14.4
Mean January temperature (°C)		- 3.2
Annual precipitation (mm)		2730
Mean snow pack February 28 (m)		3.5
Growing season (frost-free days)		130

#### Biomass Distribution

Tree biomass was calculated from regressions on stem diameter. Regressions were developed following destructive analysis of individual trees. Regressions used for the young stand are from Grier and Milne (1981); those used for the mature stand from Gholz et al. (1979). Understory biomass was estimated by

destructive sampling of plots of known area in late July. Biomass of fallen logs and standing dead trees was determined by area sampling using procedures described by Grier (1978). Forest floor biomass was obtained by area sampling. Soil organic matter concentrations were determined on soils including gravel using the Walkley-Black procedure (Jackson 1958); bulk density was then used to convert concentration to mass/area.

#### Net Primary Productivity

Net primary productivity (NPP) was calculated after measuring the various components of the equation

$$NPP = \Delta B + D$$

where  $\Delta B$  is the annual increment of living biomass and  $D$  is production of detrital material. The aboveground components of  $\Delta B$  were stem and branch increment as well as leaf biomass increment in the young stand; belowground  $\Delta B$  was coarse root increment. Aboveground detritus production consisted of litterfall, branchfall, and tree mortality. Belowground  $D$  was coarse root mortality and fine root and mycorrhizae turnover.

Above- and belowground biomass increment was calculated by difference. Biomass was calculated using regressions of component biomass on stem diameters at the beginning and end of a measurement interval; the difference between the two biomass values was taken as  $\Delta B$ .

Aboveground detritus production was determined by measuring litterfall and tree mortality. Fine litterfall was caught in 48, 0.25 m<sup>2</sup> litter traps in the mature stand and 96, 0.05 m<sup>2</sup> litter traps in the young stand. Branchfall was measured on eight 30 m<sup>2</sup> subplots in each stand. Tree mortality was obtained by annual checks of trees previously recorded as alive. Mortality biomass was calculated from regressions on stem diameter. Shrub biomass increment was negligible so shrub productivity was estimated as leaf and fruit production. Herb production was assessed by sequential harvest of small plots through the growing season.

Fine root turnover was determined by sorting roots from intact soil cores obtained periodically through the year. Roots were segregated by soil horizon and size. Soil horizon categories were: forest floor, A-horizon, and B-horizon. Size categories were: mycorrhizae, 0-2 mm diameter fibrous-textured roots and 2-5 mm diameter fibrous-textured roots. Statistically significant ( $p < 0.05$ ) decreases in fine root biomass were considered as turnover. Turnover was summed for the year in which it occurred.

#### Root Growth and Physiology Experiments

An intensive study of factors influencing root growth and general physiology of *Abies amabilis* was conducted as part of the overall study of *Abies amabilis* zone forests. These are described in detail by Teskey (1982).

In one experiment the relation between root growth and nitrogen nutrition of *Abies amabilis* was examined; results of this experiment are relevant to this discussion. In this study, 2-year-old trees were dug

in late fall and transferred to well-aerated, 10°C, 2-liter solution culture tanks containing Hoaglands solution with  $\text{NH}_4\text{-N}$  concentrations ranging from 2 to 102 ppm. The seedlings were maintained in the tanks through a growing season (10 weeks) with weekly changes of solution.

Only growth which occurred during treatment was considered as a treatment effect. The following factors were measured: area, weight, net photosynthesis and respiration of foliage; and length, weight and respiration of roots which grew during the experiment.

In a second experiment, oxygen concentrations in the rooting medium were maintained at 3%, 10%, or 21%  $\text{O}_2$ , 52 ppm  $\text{NH}_4\text{-N}$ , and 10°C. Oxygen concentrations were determined using a Clark probe. Again, area, weight, net photosynthesis and respiration of new foliage; and length, weight and respiration of new roots were determined.

## Results

Vertical distribution of living and detrital biomass is shown in Table 2. All values are reported as they were determined in mid-October 1978 except shrub and herb layer biomass; values given for these are as determined in early August.

Table 2.--Summary of biomass distribution in 23- and 180-year-old *Abies amabilis* stands in the Findley Lake research area. Data from Grier et al. (1981).

	23-year-old	180-year-old
<b>Trees</b>		
Foliage	13,640	21,650
Stem and branch	35,410	423,880
Total	49,050	445,530
<b>Shrub</b>	3,800	110
<b>Herbaceous</b>	360	60
Total aboveground living	53,210	445,700
<b>Roots</b>		
>5 mm	15,500	124,920
<5 mm	9,240	12,790
Total belowground living	24,740	137,710
Total vegetation	77,950	583,410
<b>Detritus</b>		
Forest floor	47,800	149,500
Woody detritus	82,400	239,900
Total	130,200	389,400
<b>Soil</b>	219,900	273,000
Ecosystem total	428,050	1,247,510

Leaf, fine root, wood, bark, and detritus biomass were all greater in the mature than in the young stand. Understory biomass was greater in the young stand. Epiphytes were a significant canopy component in the mature stand but were absent from the young stand. Fine roots including mycorrhizae were a small proportion of total ecosystem biomass: 2.2% of total biomass

in the young stand and 1.0% in the mature stand. On the other hand, roots were 11.8% of living biomass in the young compared to 2.2% in the mature stands.

Figure 1 shows details of the vertical distribution of fine roots in the two ecosystems studied. There appears to be a distinct shift in root distribution with increasing stand age. In the young stand, 70% of the fine roots were located in mineral soil horizons. In the mature stand, over 55% of the fine roots were in the forest floor (O1 + O2 horizons). This shift in root distribution was associated with a threefold increase in forest floor biomass.

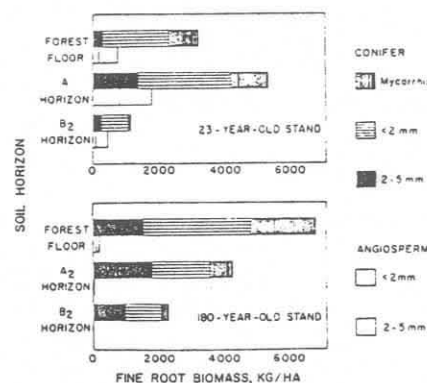


Figure 1.--Vertical distribution of fine root biomass in 23- and 180-year-old *Abies amabilis* stands. Biomass values are typical for late September.

Figure 2 shows seasonal fluctuations in conifer fine root biomass in both the young and mature stands. The data in Table 2 are a smoothed composite of three years observation of fine root biomass and show patterns for mycorrhizal roots plus the 0-2 mm fibrous-textured roots. Year-to-year variation in values for the spring peak was large. For example, in the mature stand, the peak value for spring fine root biomass was over 8000  $\text{kg ha}^{-1}$  for 1978, but only 6200  $\text{kg ha}^{-1}$  for 1980. Variation in the young stand was similar in magnitude. In spring of 1979 no spring peak was observed in either stand, meaning either that it did not occur, or that it occurred during the 6-week period between samplings that year. Fall peaks and summer and winter depressions in fine root biomass of both the young and mature stands were relatively constant; year-to-year variation was about  $\pm 15\%$  of the mean. We interpreted statistically significant increases in fine root biomass as productivity--decreases were considered as turnover.

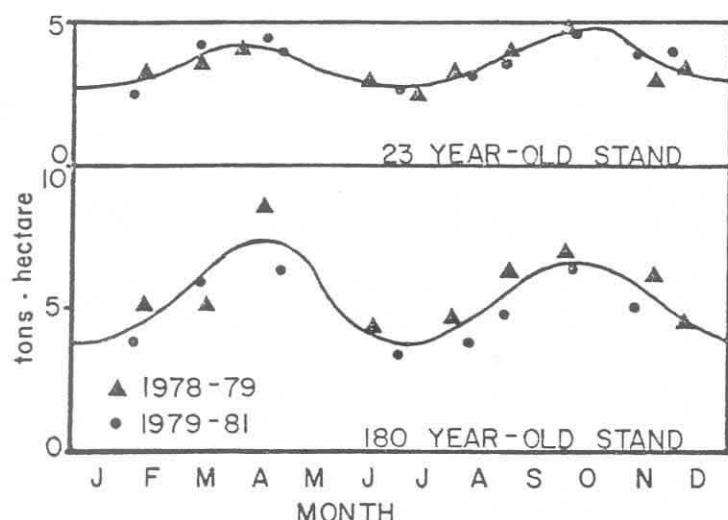


Figure 2.--Seasonal changes in conifer fine root (<2 mm) biomass in 23- and 180-year-old *Abies amabilis* stands. Data are smoothed composites of 3 years observations. Standard errors (not plotted) are less than 10% of means for all sampling dates.

In Table 3, estimates of fine root production are combined with other components of net primary productivity. Total dry matter production by the young stand is 1.03 times that of the mature stand in spite of smaller leaf biomass. Differences in aboveground net

Table 3.--Above- and belowground net primary production in young and mature *Abies amabilis* stands. Data are from Grier et al. (1981) with mortality updated.

	23-year-old	180-year-old
<b>Aboveground</b>		
Biomass increment		
leaf	220	----
wood and bark	4,100	2,320
Total	4,320	2,320
Detritus production		
litterfall	1,510	2,180
mortality	300	940
herb layer turnover	320	50
Total	2,130	3,170
Total aboveground	6,450	5,490
<b>Belowground</b>		
Biomass increment	1,780	700
Conifer fine root turnover	6,560	11,140
Angiosperm fine root turnover	3,480	390
Total belowground	11,820	12,230
Net Primary Production	18,270	17,720

production were greater; aboveground production by the young stand being 1.2 times that of the mature stand.

The small difference in total net production compared with a relatively large decrease in aboveground

production are the result of a shift from above- to belowground production with age. Production of conifer fine roots including mycorrhizae was 6560 kg ha<sup>-1</sup> in the young and 11,140 kg ha<sup>-1</sup> in the mature stand. As a proportion of total net productivity, conifer fine roots and mycorrhizae were 35.9% in the young and 62.9% in the mature stand. Of course understory vegetation contributed about 35% of total net production in the young stand. But in spite of this, fine root production including angiosperms was still only 45% of total young stand dry matter production.

Table 4 shows the levels of mineral nitrogen present in the soil profile of both the young and mature stands. The values of mean extractable N represent the average amounts of mineral N present in the various horizons of an undisturbed soil profile during the growing season. The incubation N values are an index of the rate of N mineralization in the various horizons. Values given in Table 4 are for NH<sub>4</sub>-N only; NO<sub>3</sub>-N was an insignificant proportion of total mineral N in all determinations.

Table 4.--Mineral nitrogen in forest floor and soil of young and mature *Abies amabilis* stands at the Findley Lake research area. Standard errors are in parentheses. Mean extractable nitrogen is the mean of all growing season samples; samples were taken every 10 days from 1 June 1979 to 30 September 1979. NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>, extracted in 2N KCl and analyzed using procedures described in Vitousek et al. (1982). Incubation N is the concentration of 2N KCl extractable NH<sub>4</sub> in the forest floor and soil after an 8-week incubation at 20°C and field moisture capacity (-0.1 bar). Nitrate concentrations were consistently < 0.5 ppm in forest floor and < 0.1 ppm in soil.

	ppm	
	Mean extractable N	Incubation N
<b>23-year-old Stand</b>		
Forest floor	45.2 (3.7)	91.2 (7.2)
0-15 cm (A horizon)	5.1 (0.4)	26.4 (1.6)
15-70 cm (B horizon)	1.3 (0.1)	4.8 (0.3)
<b>180-year-old Stand</b>		
Forest floor	38.0 (3.6)	62.0 (4.7)
0-15 cm (A horizon)	4.4 (0.3)	6.3 (0.05)
15-70 cm (B horizon)	0.8 (0.1)	2.1 (0.01)

Mean extractable N levels in the young stand averaged about 20% greater than those in the mature stand for all soil horizons. On the other hand, N mineralization potential, as indicated by incubation, was considerably greater in the young stand than in the mature stand, especially in the A-horizon. Here, N mineralization was roughly five times that of the A-horizon of the mature stand. This difference in mineralization rates under incubation conditions amounts to 2.1 kg ha<sup>-1</sup> more NH<sub>4</sub>-N being produced in the young than in the mature stand over a 10-week interval in the A-horizon alone.

Table 5 shows the response of small *Abies amabilis* to different concentrations of N in their growing solution. Initial concentrations ranged from 2 to 102 mg l<sup>-1</sup>. Solutions were changed weekly for a 10-week period. Thus the total amount of N supplied to the root systems ranged from 20 mg to 1020 mg over the period of the experiment.

Table 5.--Fine root and foliage response to a range of nitrogen availability, root zone oxygen concentration, and root temperature. Ratios and amounts represent only new foliage and new root growth. Data from Teskey (1982).

Treatment	Foliage wt. (mg)	Root wt. (mg)	Root foliage (ratio)	Root root + foliage (ratio)
<b>Nitrogen</b>				
102 ppm	478 <sup>a</sup>	73 <sup>a</sup>	0.15 <sup>a</sup>	0.13
52	417 <sup>a,b</sup>	79 <sup>a</sup>	0.19 <sup>b</sup>	0.16
22	344 <sup>b,c</sup>	73 <sup>a</sup>	0.21 <sup>b</sup>	0.18
2	266 <sup>c</sup>	42	0.16 <sup>a</sup>	0.14
<b>Oxygen</b>				
21%	484 <sup>a</sup>	134	0.28	0.22
10	406 <sup>a</sup>	39 <sup>a</sup>	0.09 <sup>a</sup>	0.10
3	274	30 <sup>a</sup>	0.11 <sup>a</sup>	0.10
<b>Temperature</b>				
20°C	429 <sup>a</sup>	99 <sup>a</sup>	0.23	0.19
10	454 <sup>a</sup>	80 <sup>a</sup>	0.18 <sup>a</sup>	0.15
3	481 <sup>a</sup>	56	0.12 <sup>a</sup>	0.10

Same letter in a column within each treatment (nitrogen, oxygen, temperature) denotes no significant difference at  $\alpha = 0.05$  (Duncan's multiple range test).

Table 6 gives the response of young *Abies amabilis* to various root zone temperatures, O<sub>2</sub> and NH<sub>4</sub>-N concentrations. The trees maintain basically the same photosynthetic rate regardless of temperature; root respiration decreased with decreasing soil temperature. Photosynthesis dropped markedly at O<sub>2</sub> levels below 10% and NH<sub>4</sub>-N levels below 22 ppm.

Effects of various NH<sub>4</sub>-N and O<sub>2</sub> levels and temperature are more obvious when foliage plus root respiration is expressed as a proportion of photosynthesis. At low N and oxygen levels and high temperatures, respiration utilized over 90% of photosynthate produced. Soil O<sub>2</sub> levels appear to have the greatest effect on the ratio; reducing root atmosphere from 21% to 10% O<sub>2</sub> increased the respiration/photosynthesis ratio from an about-average 0.69 to 0.89. We routinely measure soil atmosphere O<sub>2</sub> concentrations <10% under field conditions, especially in summer and fall when soil temperatures approach 10°C (Grier unpublished data, Hinckley unpublished data).

Table 6.--Photosynthesis and respiration response by small *Abies amabilis* to different nitrogen, oxygen, and temperature regimes. Data from Teskey (1982).

Treatment	Photosynthesis mgCO <sub>2</sub> h <sup>-1</sup> per plant	Foliage respiration mgCO <sub>2</sub> h <sup>-1</sup> per plant	Root respiration mgCO <sub>2</sub> h <sup>-1</sup> per plant	Net photosynthesis total resp.
<b>Available nitrogen (NH<sub>4</sub>-N) <sup>1/</sup></b>				
102 ppm	2.30 <sup>a,1/</sup>	1.25	0.36 <sup>a</sup>	0.70
52	1.87 <sup>a</sup>	0.94 <sup>a</sup>	0.34 <sup>a</sup>	0.68
22	1.57 <sup>a</sup>	0.93 <sup>a</sup>	0.37 <sup>a</sup>	0.76
2	0.84	0.56	0.22 <sup>a</sup>	0.93
<b>Root zone oxygen <sup>2/</sup></b>				
21%	2.32 <sup>a</sup>	1.37 <sup>a</sup>	0.52	0.69
10	1.93 <sup>a,b</sup>	0.97 <sup>a</sup>	0.63	0.89
3	0.84	0.66 <sup>a</sup>	0.12	0.93
<b>Root temperature <sup>3/</sup></b>				
20°C	1.97 <sup>a</sup>	1.08 <sup>a</sup>	0.82	0.95
10	2.16 <sup>a</sup>	1.07 <sup>a</sup>	0.46	0.71
3	2.08 <sup>a</sup>	1.28 <sup>a</sup>	0.12	0.67

<sup>1/</sup> Same letter in a column within each treatment (nitrogen, oxygen or temperature) denotes no significant difference at  $\alpha = 0.05$  (Duncan's multiple range test).

<sup>2/</sup> 10°C, 21% O<sub>2</sub>.

<sup>3/</sup> 10°C, 52 ppm NH<sub>4</sub>-N.

<sup>4/</sup> 52 ppm NH<sub>4</sub>-N, 21% O<sub>2</sub>.

## Discussion

Earlier in this paper, we stated that our original objective was to test the hypothesis that immobilization of mineral nutrients in accumulating detritus would cause a progressive loss of soil fertility as these subalpine forests mature. We further postulated that trees would respond to the resulting decline in nutrient availability through increased fine root biomass increased production and turnover of fine roots and greater reliance on mycorrhizae.

None of the research reported in this paper can be considered as a rigorous test of our hypothesis. Several, potentially interacting, factors appear to influence root distribution and growth.

Clearly, N availability in the mature stand is less than that of the young stand (Table 4). Moreover, N availability and N mineralization rates in both the young and mature stands are less than those reported for many other forest soils in the United States (Vitousek et al. 1982).

Fine root biomass of the mature stand is greater than that of the young stand (Table 2). In addition, fine roots of the mature stand are concentrated in the forest floor; those of the young stand in the A-horizon of the mineral soil (fig. 1). Root concentration appears to occur in soil horizons having the highest mineralization rates on a mass per unit basis.



Patterns of production and turnover of fine roots tend to confirm the nutritional hypothesis. While production of fine roots is a much larger proportion of net primary production in the mature stand than in the young stand (Table 3), N mineralization rates and amounts are greater in the young stand than in the mature stand. Fine root production in these stands is also greater than in lowland Douglas-fir stands where N-availability is greater (Keyes and Grier 1981, Vitousek et al. 1982).

The dominance of the ammonium form of mineral N in these ecosystems would tend to encourage rapid root turnover and dense rooting in soil horizons where N mineralization is occurring. Ammonium tends to be relatively strongly sorbed on cation exchange sites. For this reason, movement of ammonium ions along a diffusion gradient is a slow process requiring the presence of a counterdiffusion cation (Barber 1974). This appears to restrict diffusion of ammonium toward plant roots to relatively short distances. Thus in soils where ammonium is the dominant form of mineral N, but where ammonification proceeds slowly, it appears as if sufficient mineral N could be obtained only if root systems dynamically explore the soil.

In spite of evidence suggesting that low nutrient availability is the major factor influencing root biomass, its distribution, and its production; other factors also appear to play a role. Soil oxygen, soil temperature, and soil N availability all have an influence not only on root-shoot ratios but also on the carbohydrate balance of *Abies amabilis* (Tables 4 and 5).

For example, concentration of roots near the soil surface may reflect oxygen availability more than nutrient availability. Measurements of soil respiration in the mature stand on trenched (no roots) and adjacent untrenched areas showed no significant difference in CO<sub>2</sub> production between treatments over an entire growing season. Trenched plots had been established 3 years, prior to beginning respiration measurements and were enclosed in polyethylene sheet to prevent root regrowth. One interpretation of these results is that oxygen availability limits those belowground processes involving respiration. Elimination of root systems and their oxygen requirements would simply make more O<sub>2</sub> available for utilization by decomposer organisms. Concentration of roots near the atmospheric source of O<sub>2</sub> would increase root oxygen supply. This possibility is currently under study.

At the present time, it is difficult to identify any single factor responsible for the large biomass or high production of fine roots in *Abies amabilis* ecosystems. There is good evidence suggesting the large carbon allocation to roots and mycorrhizae is related to low nutrient availability. However, we have not been able to establish a direct link between nutrition and root biomass. There are two major reasons for this. First, efforts to alter the available nutrient balance of these sites have not been notably successful. Additions of  $\text{NH}_4\text{-N}$  as urea have been made at rates up to 80 g N m<sup>-2</sup>. Within two weeks of fertilization,  $\text{NH}_4\text{-N}$  concentrations in fertilized and non-fertilized forest floors were again nearly identical. We believe that the applied N is simply being immobilized by decomposer organisms; for we could not detect increased N in tree foliage. Second, if soil oxygen levels are influencing tree root distribution, then oxygen availability could

equally well be influencing nutrient mineralization rates. Thus, a measure of caution must be used when suggesting that root production and distribution reflect nutrient availability. Before the connection can be made, the factors influencing nutrient availability must be identified.

#### LITERATURE CITED

- Barber, S.A. 1974. Influence of the plant root on ion movement in soil. P. 525-564 In Carson, E.W. (ed.). The plant root and its environment. Univ. Press of Virginia, Charlottesville, Va.
- Franklin, J.F., and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. 417 p.
- Gholz, H.L., C.C. Grier, A.G. Campbell, and A.T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Laboratory, Res. Pap. 41, Oregon State Univ., Corvallis.
- Grier, C.C. 1978. A *Tsuga heterophylla*-*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can. J. For. Res. 8:198-206.
- Grier, C.C., K.A. Vogt, M.R. Keyes, and R.L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can. J. For. Res. 11:155-167.
- Grier, C.C., and W.A. Milne. 1981. Regression equations for calculating component biomass of young *Abies amabilis* (Dougl.) Forbes. Can. J. For. Res. 11:184-187.
- Jackson, M.L. 1958. Soil chemical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 498 pp.
- Keyes, M.R., and C.C. Grier. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11:599-605.
- Krajina, V.J. 1970. Ecology of forest trees in British Columbia. P. 1-146 In Krajina, V.J. (ed.). Ecology of Western North America, Vol. 2. Univ. British Columbia, Botany Dept., Vancouver, B.C.
- Meier, C.E. 1981. The role of fine roots in N and P budgets in young and mature *Abies amabilis* ecosystems. Ph.D. dissert., Univ. of Washington, Seattle. 114 p.
- Teskey, R.O. 1982. Acclimation of *Abies amabilis* to water and temperature stress in a natural environment. Ph.D. dissert., University of Washington, Seattle. 135 p.
- Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Melillo, and W.A. Reinners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecol. Monogr. 52:155-177.
- Zobel, D.B., A. McKee, G.M. Hawk, and C.T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46:135-156.